

CAN SIMPLE EXPERIMENTAL ELECTRONICS SIMULATE THE DISPERSAL PHASE OF SPIDER BALLOONERS?

James R. Bell: Warwick HRI, Wellesbourne, Warwickshire CV35 9EF. E-mail: j.r.bell@warwick.ac.uk

David A. Bohan and Richard Le Fevre: Rothamsted Research, Harpenden, Hertfordshire AL5 2JQ

Gabriel S. Weyman: Syngenta, Jealott's Hill International Research Centre, Bracknell, Berkshire RG42 6EY

ABSTRACT. Here we describe the structure of a fall speed chamber designed to measure, with low experimental error, the terminal velocities (fall speeds) of spiders of known weight and a given length of silk. We also describe the construction of a simulated individual (SI) which could later be used to estimate the distance travelled by ballooning spiders in the field. Our data and analysis suggest that *Oedothorax* spp. (Linyphiidae) and *Pachygnatha degeeri* (Tetragnathidae) individuals have fall speeds that can be described by their silk length and mass. Of the observed deviance in the fall speeds, 73.7% could be explained by a GLM model common to both species groups. Overlaying the SI fall speed data on this GLM surface suggests that the SIs have similar fall speed behaviors to spiders. However, further estimation is necessary before SIs could be considered valid models for evaluating spider ballooning distances.

Keywords: Dispersal, ballooning, schottky diodes, silk, fall speed chamber

Ballooning research has faced a seemingly intractable question for over 300 years: how far do ballooning spiders disperse once airborne? While there have been attempts to observe ballooning distances visually, which suggest that spiders move no more than a few hundred metres in any one attempt (e.g. MacCook, 1877; Follner & Klarenberg 1995; Schneider et al. 2001), it also may be inferred from anecdotal evidence that spiders also make journeys of several hundred kilometres (Yoshimoto & Gressitt 1960; Okuma & Kishimoto 1981). However, such visual and anecdotal data are rare and have yet to yield any significant data for the great majority of ballooning spiders, including the linyphiids (Bell et al. 2005). Although models of ballooning distance have been constructed (e.g. Thomas et al. 2003), the predicted distances have yet to be verified.

The lack of progress is perhaps surprising given recent advances in radar technology (Chapman et al. 2003). Although Rothamsted Research's vertical looking radar (VLR) can measure the horizontal speed, displacement direction, body alignment, mass and shape of

flyng insects up to 1 km above ground level (Chapman et al. 2003), as yet ballooning spiders cannot be uniquely identified. The VLR fails to resolve ballooners because spiders lack distinctive allometric ratios and tend to have masses near or below the critical threshold for the radar (Chapman et al. 2003; Jason Chapman pers. comm.).

Recently, indirect molecular genetic techniques have been employed as an alternative to measuring airborne spiders directly (Goodacre 2004). This approach was designed to detect the effect of dispersal rates on the genetic diversity of a number of key linyphiid populations across the British mainland and its islands. The research has shown that populations on islands have lower genetic diversity than those found on the mainland, implying changes in gene flow with isolation distance and island size. It should be noted however, that these findings were not independent of *Wolbachia* infections which confounded observed gene flow measurements. Other molecular studies, which indirectly estimate ballooning distance using gene flow, have been conducted (as reviewed by Bell et al. 2005)

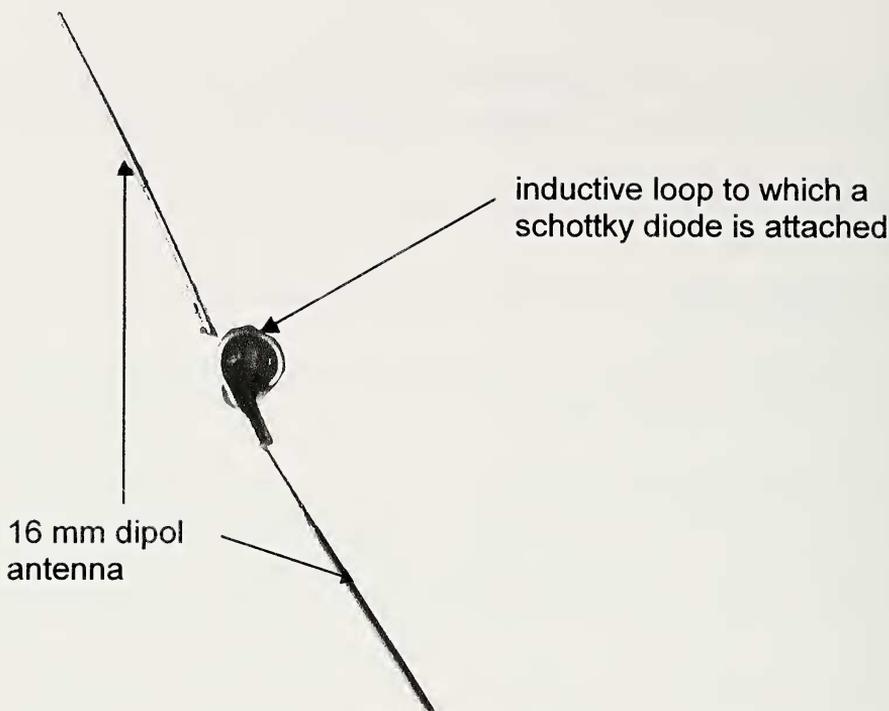


Figure 1.—A simulated individual, which shows a 16mm dipole antenna attached to an inductive loop. The 0.3mm schottky diode (not visible) is fixed to the inductive loop using gold spatter technology. The complete unit weighs 8mg.

but have not yielded estimates for the distances travelled by individual spiders.

We present an alternative approach, based upon synthetic models for spiders that we term simulated individuals (SI). SIs show great promise because they are traceable and biologically inert, thus resolving problems of airborne detection and *Wolbachia* infection. However, while we have begun to understand the physical properties of spiders and their implications for ballooning (Suter 1991, 1992, 1999), the properties of SIs are unknown and their comparative behavior remains untested. In this paper, a description of the technology and data used to compare SI properties against spiders is presented, concluding with a discussion of future research prospects for ballooning.

METHODS

Simulated individuals and spiders.—

Males and females of *Oedothorax* spp. (mixed *apicatus*, *fuscus* and *retusus* species: Linyphiidae) and *Pachygnatha degeeri* (Tetragnathidae) have been recorded ballooning many

times (see world catalog in Bell et al. 2005). These species were used as model ballooners for comparison with a simulated individual (SI). While the properties of an SI are yet to be established, the desirable traits should be that it: i) is structurally similar to a spider, consisting of a body and an associated silk component; ii) is able to generate its own drag to enable it to become airborne; iii) is traceable, producing an automated signal of its location; iv) allows manipulation of the silk component to known levels of drag; and, lastly v) is a 'null' spider with no behavior which minimizes drag variability (i.e. absence of biting and reeling of the silk line and reduced body posture modification). Schottky diodes, mounted onto an inductive loop with a dipole antenna (referred to as 'diodes' hereafter) have the potential to offer these properties, despite having none of the physical attributes of spiders (Fig. 1). We used 8 mg diodes in the following experiments.

Spiders create drag with single or multiple silk lines that may account for 75% of the total drag of the spider (Humphrey 1987). For

the diodes, simulated silk was adopted initially as a replacement for natural silk. Titanium-coated fibre glass was identified as a possible solution and responded positively to very light convection currents (i.e. < 1 m/s). However, it proved to be fragile despite being four times the diameter (400 nm) of natural linyphiid silk (e.g. *Tenuiphantes tenuis* 100 nm). In light of these flaws, we used natural silk. Although linyphiid silk is too fine to manipulate easily, it was possible to attach the drag line silk of immature *Araneus diadematus* (Araneidae) to the diodes. For both spiders and diodes, all individuals were weighed before being introduced to the Rothamsted fall speed chamber described below. In total, 38 spiders (*Oedothorax* spp. $n = 13$; *P. degeeri* $n = 25$) and 4 diodes were dropped attached to silk lengths within the range of 0–2.3 m.

Rothamsted fall speed chamber.—The physical structure of the 9 m vertical chamber was relatively simple and included three detector stages and a hotwire (Fig. 2). The hotwire was used as a silk-shearing mechanism to allow suspended spiders to be dropped without human intervention. The first detector stage was used to manipulate the silk length, between 0.11 m and 2.3 m, at which a suspended spider or diode entered free fall and the two remaining stages measured the fall speed of each individual having reached terminal velocity. As a precursor to entering the chamber, spiders were first prompted to drop down on a drag line from an oscillating probe. Having produced a dragline of >10 cm, spiders were then fixed to the hotwire and allowed to pay out more silk until triggering the first detector stage (Fig. 3). In separate experiments, the diodes were suspended on fixed lengths of silk placed on the hotwire. The silk was sheared by one of two methods: either a) the spider broke the first detector stage light beam which automatically triggered the hotwire (Figs. 2 & 3); or, b) if shorter lengths of silk (i.e. < 0.11 m), silkless drops or fixed drops with diodes were required, a PC-operated drop mechanism which manually triggered both the three detector stage light beams and the hotwire to an 'on' position was used. After either the hotwire or manual drop had been triggered, the spider or diode entered free fall for at least 5.4 m (i.e. depending on the first detector stage height) until it was measured passing through the second detector

stage at terminal velocity when timing started (Fig. 2). Timing was stopped, and the fall speed computed, when the individual passed through the third detector stage.

The hardware environment behind the fall speed chamber measurements is based on the simple principle that when an object breaks a light beam, a passive record can be logged at a given point in time. Technically, the chamber included its own microprocessor controller based on a PIC16F876 running at 20 MHz and programmed using CCS PICC compiler (Fig. 4). This controller was connected to a PC running dedicated software through a RS232 port, which allowed the user to control the light source and silk release mechanism (i.e. automatic/manual release) remotely. All control outputs were by opto-isolated open drain mosfet drivers. The hardware detected falling objects through the use of a medium area photo diode (41.3 mm²) connected to a two stage high gain amplifier. A first order bandpass filter was used to remove unwanted signals below 300 Hz and above 5 KHz. The photo diode was mounted in a black box, with one end cut off, to help prevent ambient light interfering with the source light. The initial design for the detection system was to incorporate a laser diode with line generator lens as the light source. However, the tested lasers were found to have a small but significant fluctuation in their output which made it impossible to distinguish the object signal from noise when used in conjunction with the detection circuit. The circuit will need to be redesigned before lasers can be used in this application.

As an alternative, high power quartz halogen bulbs (60 W) were used in conjunction with two 0.8 mm slits spaced at about 160 mm apart so that a reasonably fine line beam could be produced (Fig. 5). To focus the light onto the photo diode, Fresnel lenses (~ 300 mm wide, cut from a 280 mm square lens along the diagonal, 50 grooves per inch and a focal length of 234 mm) were employed. The signal from the photo diode was then amplified and filtered before being applied to the single input channel of the analogue switch driven by a free running 3 KHz quartz clock (Fig. 4). The two output channels of this switch were then applied to the inputs of the voltage comparator. Any low frequency variation of the input signal due to amplifier drift or ambient light falling on the photo diode was ignored

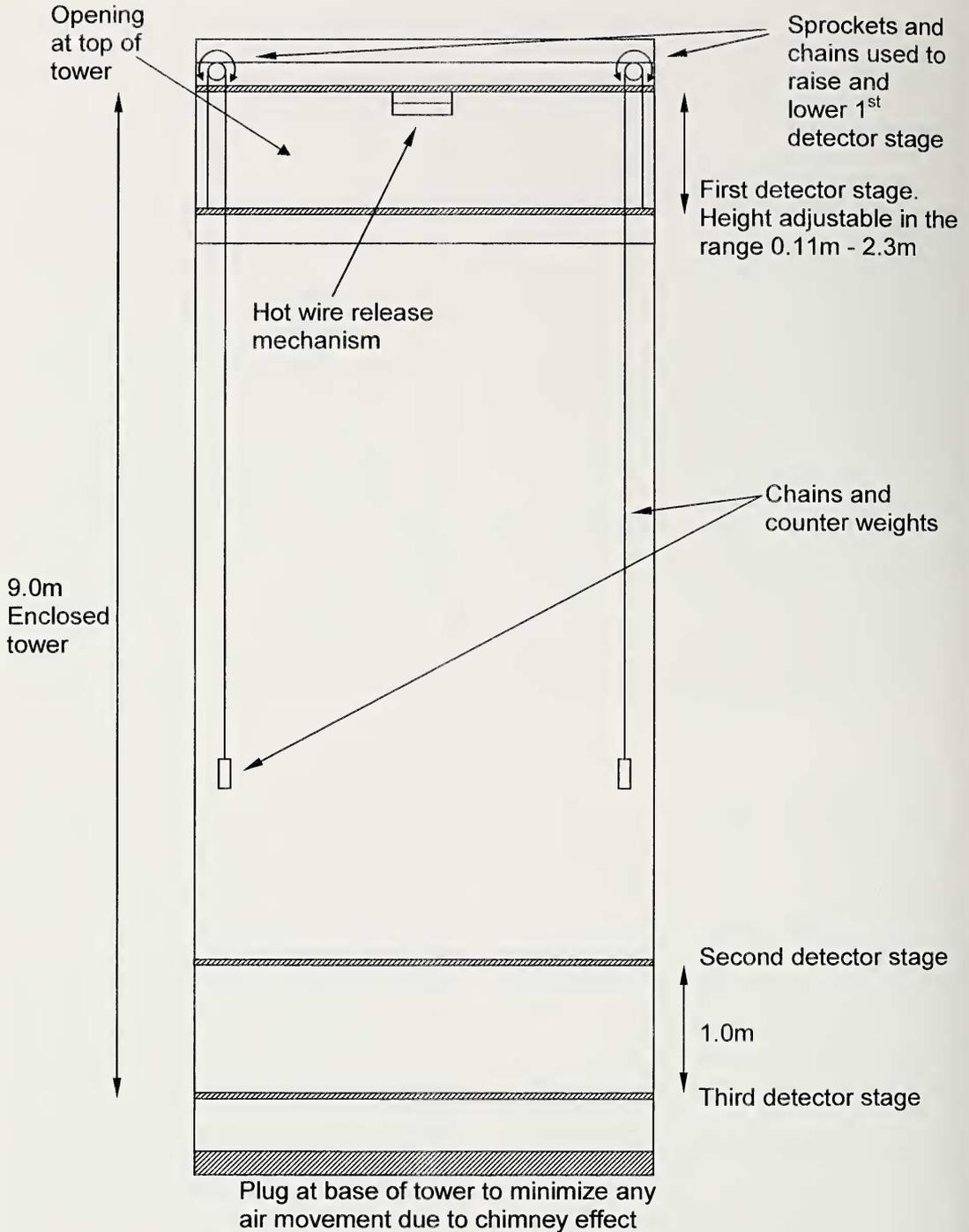


Figure 2.—Side view of the Rothamsted fall speed chamber.

by the comparator. However, any object passing through the light beam produced a much faster change in signal level which triggered the comparator. The comparator output was used

as the trigger input to the microprocessor controller. The inherent precision of the microprocessor quartz clock ensured that the accuracy of the system fell within at least ± 1 ms

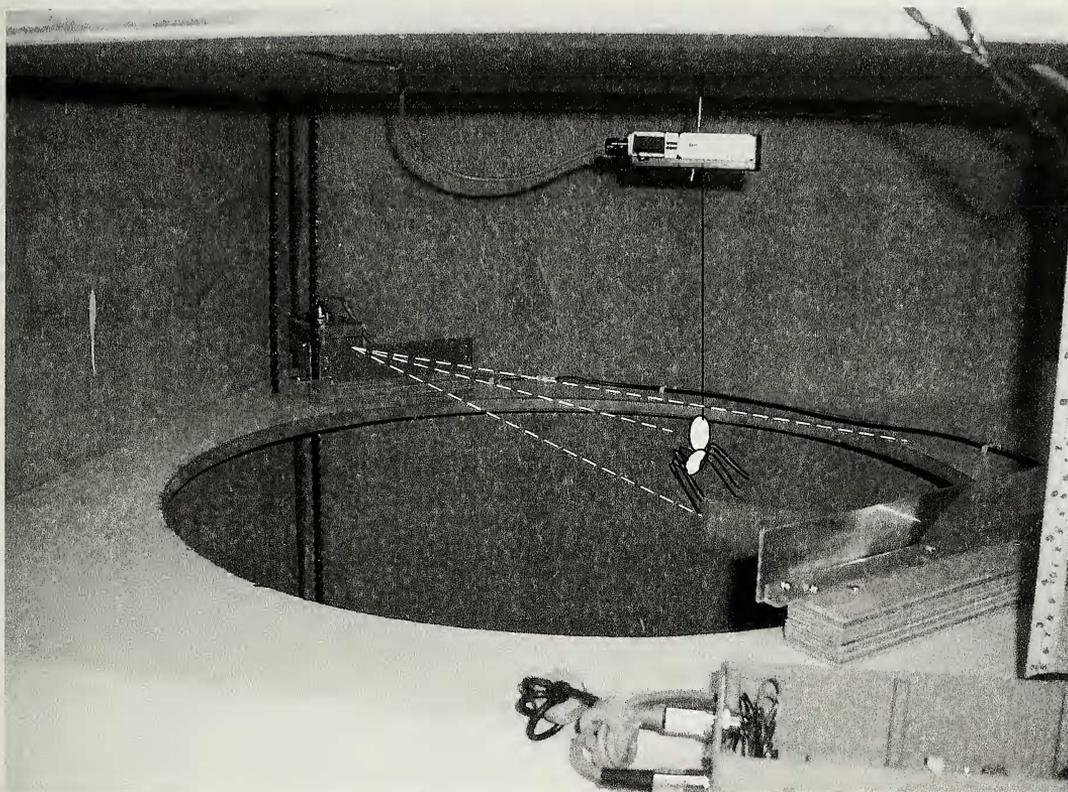


Figure 3.—Top of Rothamsted fall speed chamber showing the hotwire release mechanism to which a spider is suspended on a silken line.

(accuracy checked against a calibrated Systron Donner counter timer type 6250A) and represented a fall time recorder error of the spiders sampled between 0.0046–0.055%.

Statistical analysis.—Fall speeds were analyzed using a Generalized Linear Model (GLM), the Normal distribution and the log-link function in Genstat (version 6, VSN international, Oxford, UK; McCullagh & Nelder 1989). $\log_{10}(\text{Silk Length} + 1)$ was fitted in the model as the explanatory variable, with spider species and $\log_{10}(\text{Spider Mass})$ as covariates. The model fit was checked for overdispersion in the data (McCullagh & Nelder 1989). The model's standardized residuals were checked for linearity, leverage and homogeneity (McCullagh & Nelder 1989). No attempt was made to fit a GLM to the provisional data for the diodes.

RESULTS

The GLM was found to fit the spider fall speed data extremely well, explaining some

73.7% of the GLM deviance observed (Fig. 6). The data were found to be underdispersed, suggesting that the data were more regularly distributed than expected for data conforming to the Normal distribution. An empirical scale parameter was used to adjust the model fitted estimates of error to account for this underdispersion (see McCullagh & Nelder 1989).

Spider fall speeds were found to decrease with increasing silk length ($t_{1,36} = 2.87$, $P = 0.004$) and increase with an increase in spider body mass ($t_{1,36} = 3.25$, $P < 0.001$). There was no interaction between silk length and spider body mass ($t_{1,36} = 0.28$, $P = 0.78$). No difference in the GLM was found with spider species ($t_{1,36} = 0.70$, $P = 0.49$), and no interaction was found between spider species and silk length ($t_{1,36} = 0.62$, $P = 0.53$) nor spider weight ($t_{1,36} = 1.31$, $P = 0.19$). Thus, a common GLM was applicable to both *Oedothorax* spp. and *P. degeeri*:

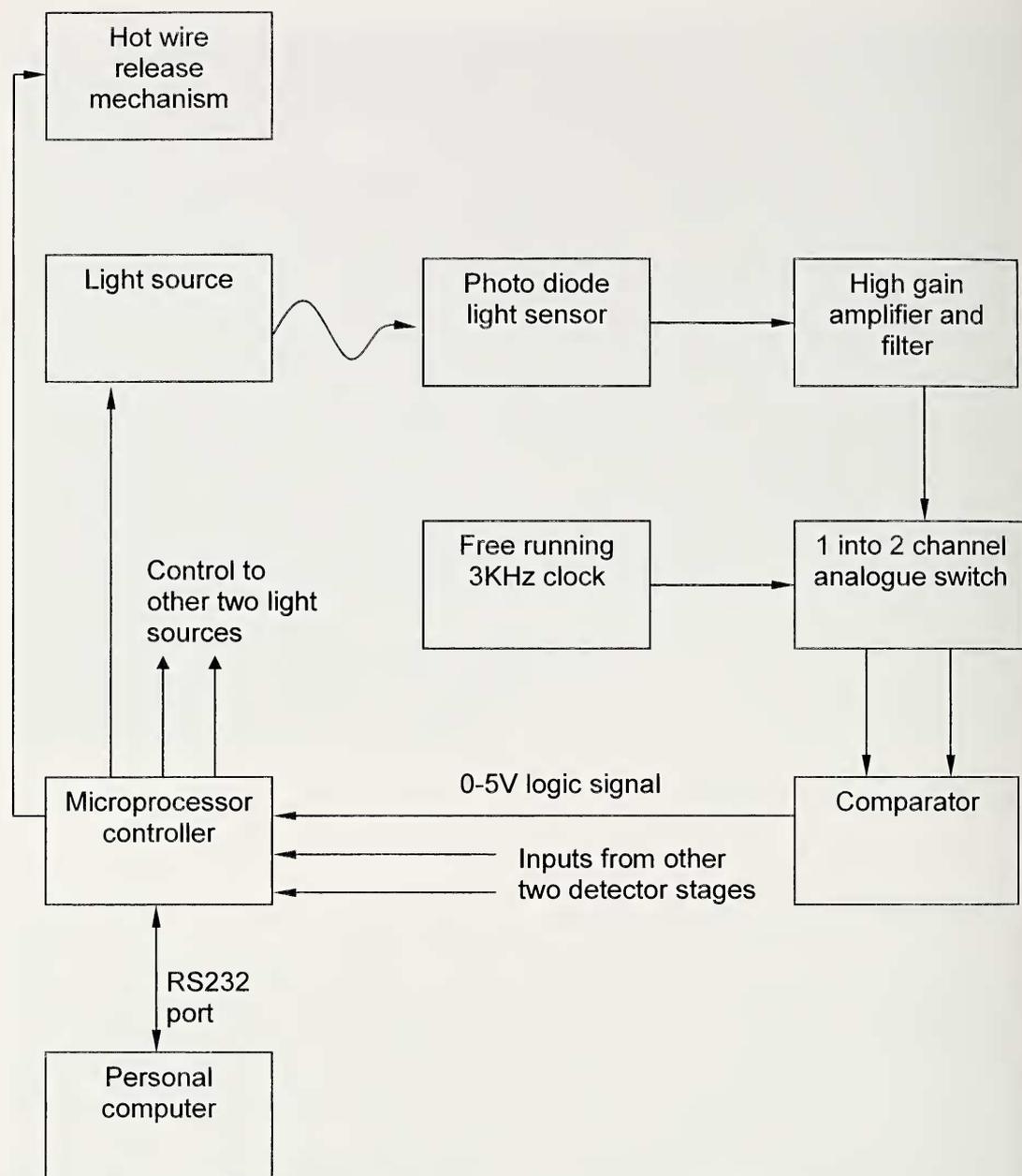


Figure 4.—Block diagram detailing system electronics.

$$\log_{10}(\text{Fall Speed}) = 3.83$$

$$- 0.95\log_{10}(\text{Silk Length} + 1)$$

$$+ 1.11\log_{10}(\text{Spider Mass})$$

Spider sex was a non-significant model covariate ($t_{1,36} = 0.06$, $P = 0.95$). However, the *Oedothorax* spp. are sexually dimorphic

with respect to weight (females = 2.4 ± 0.3 mg; males = 0.8 ± 0.004 ; $F_{1,11} = 50.14$, $P < 0.001$), yielding sex specific fall speeds for a given silk length in this species group. We plotted the fall speeds for diodes over the GLM in Fig. 6. The overlaid data suggests that diodes behave in a manner that is analogous to the spiders.

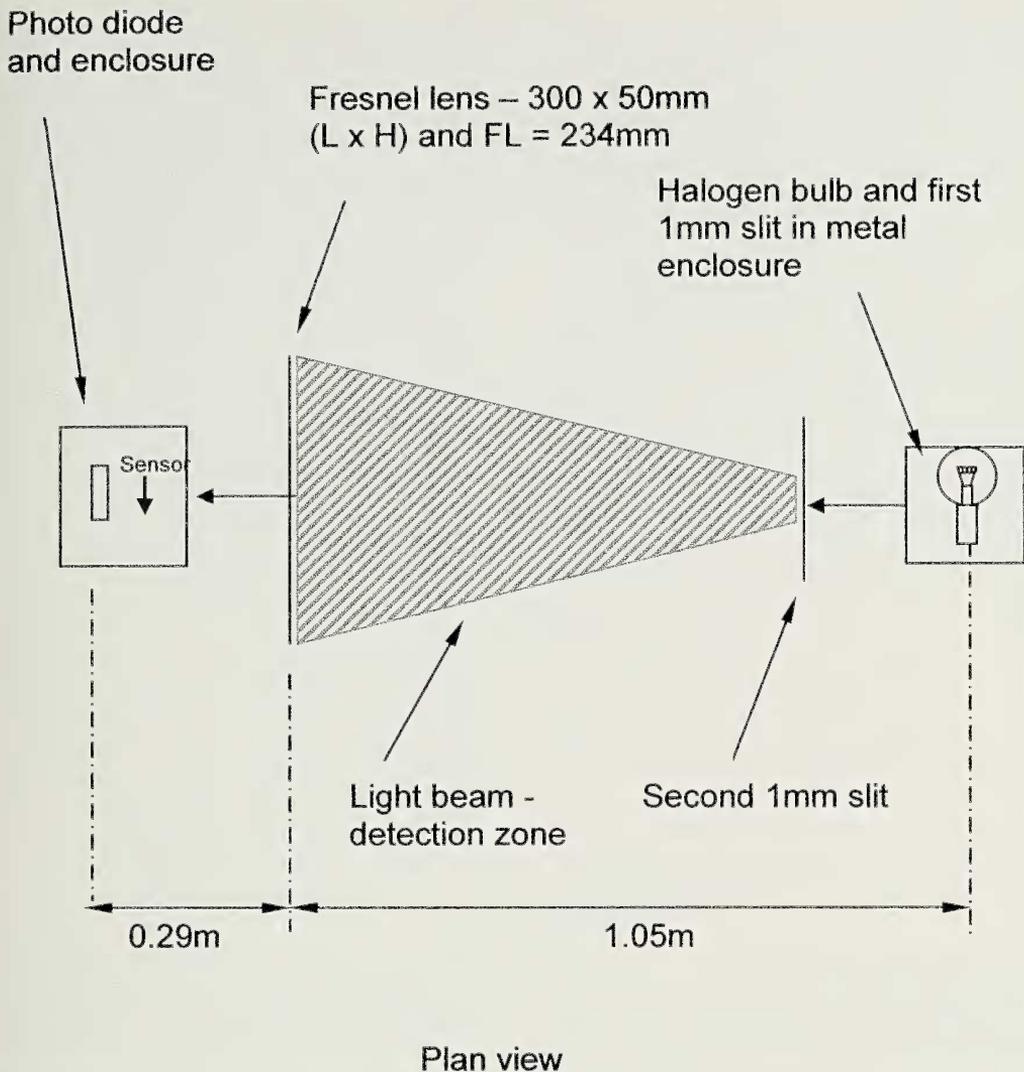


Figure 5.—Diagrammatic view of the filtered light source (←) producing a large detection zone which is constantly monitored by the photo diode.

DISCUSSION

Rothamsted fall speed measurements.—

This experiment unequivocally demonstrates that natural spider silk can be attached to diodes and that drag, and consequently fall speeds, can be systematically manipulated through the length of the silk line. The observed positive relationship between drag and silk length for SIs was analogous, but not identical, to spiders in free fall. Despite the limits of the provisional data presented, our results are supportive and imply that these diodes represent a simple, yet viable paradigm of real spiders. Encouragingly, these diodes

have the potential to develop our understanding of spider ballooning far beyond our present knowledge.

Spider ballooning research is limited, although scientists are aware of the importance of silk in ballooning (Bell et al. 2005). For example, the effect of silk length on the fall speeds of spiders (Suter 1991), moth larvae (Lepidoptera) (Batzer 1968; Barel 1973; Mitchell 1979; McManus & Mason 1983; Ramachandran 1987) and spider mites (Tetranychidae) (Jung & Croft 2001) has already been demonstrated. Of these, Suter's (1991) seminal research attempted to evaluate fall

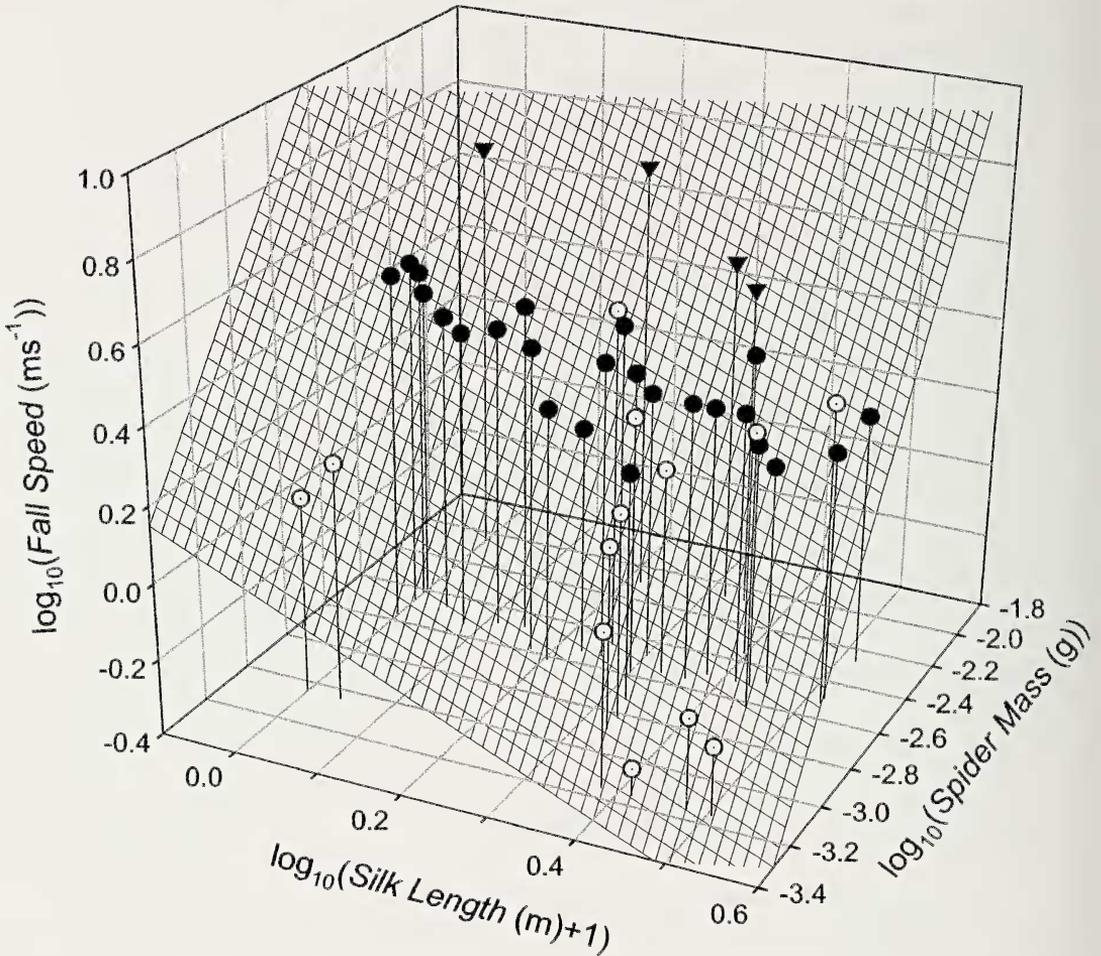


Figure 6.—Observed fall speed data for individuals of *Pachygnatha degeeri* (●), *Oedothorax* spp. (○) and diode (▼) against silk length and spider mass. The hatched surface represents the GLM fitted model for fall speeds with silk length and spider mass.

times independently of human error. Even so, fall speeds still had to be estimated by extrapolation because of the short fall distances in Suter's experimental chamber. The advantages of the Rothamsted fall speed chamber are that measurements may be taken in near-still air conditions and when they have reached their terminal velocity, after individuals have fallen at least 5.4 m. Despite this, the results are subject to error due to spider behaviors when falling. Here no attempt was made to control for postural variation, such as spreading or withdrawing legs, which has been estimated to have up to a 10 fold effect on body drag (Suter 1992). Postural control may also be important in mites which manipulate drag in a similar fashion to spiders and may be able to

influence where they land (Jung & Croft 2001). Such postural control could account for some of the unexplained variation in our GLM and may be estimated by placing digital cameras inside the Rothamsted fall speed chamber. The posture of the photographed spiders, once categorized by shape, might then be included as a third covariate within the GLM. However, this behavior might only be expected to account for a maximum of 25% of the observed variation (deviance) in the fall speed data (Suter 1991; see also Humphrey 1987).

Allowing spiders to reach their terminal velocities over a comparatively large distance simplifies the mathematics of calculating terminal fall speeds, but also has the potential to be biologically erroneous. Purely from obser-

vation during handling, both species tested were able to pay-out silk at a rate of >1 m/s, particularly when individuals adopted 'escape' behaviors. If this paying-out of silk occurred during freefall, then the lightest individuals could produce several meters of 'undetected' silk length during their fall. In practice this is unlikely, given that the residual variation was relatively small. While it is important to highlight posture and silk reeling as sources of error, they are inescapable covariates of spider ballooning. Posture variation might be standardized, though not removed, by anaesthetising individuals with carbon dioxide before entering the chamber (Jung & Croft 2001). However, this would have an impact on an individual's ability to produce silk. The solution to evaluating the effects of posture and variation in silk length during freefall can only be to increase the number of observations (replicates).

Suter (1991, 1992) recognized the importance of spider mass, which served to increase the fall speeds at a given length of silk. Mathematical models which seek to determine the probability of dispersal based on a species by species account, also need to parameterize mass and consider sex as a covariate where obvious differences in males and females occur. As far as we are aware, this has been ignored to date.

The future of schottky diodes to simulate the dispersal phase of spider ballooners.—This research has shown that simulating ballooners has potential. Natural silk attached to diode bodies produces drag in a manner directly analogous to a spider. Scanning harmonic radar has been shown to be effective in tracking diode-tagged bees for up to 900 m from the radar station (Osborne et al. 1999). To follow SIs, the use of a similar scanning radar set-up is planned. Using this technology we can explore unanswered questions including; how far do ballooners travel; and, what is the pattern of dispersal of ballooners within a 1–2 km range? However, our research is at an early stage. While releasing diodes in the field is the ultimate objective, several aspects of SI behavior need further estimation before SI ballooning data can be captured. Notably, the dependence of fall speeds on diode mass requires evaluation because the 8 mg diodes used do not represent the majority of ballooners, which are under 2 mg (Greenstone et al.

1987); although much heavier spiders can be found ballooning. Reducing schottky diode mass by at least 75% would affect the drag dramatically and could require models for SIs that differ significantly from that estimated here for spiders. Only after completion of this diode model estimation phase of the project could radar-based fieldwork follow.

ACKNOWLEDGMENTS

Thanks are due to Alan Smith, Jason Chapman, Kelvin Conrad (RR) and Andrew Mead (Warwick HRI) for their helpful discussions and advice. We also thank Ian Denholm (RR), David Skirvin and Rosemary Collier (Warwick HRI) for proof reading the MS. We are grateful for the assistance of Soeren Toft as ecology editor and thank the two peer reviewers for their comments. This paper is dedicated to the memory of Julian Haughton, naturalist and friend.

LITERATURE CITED

- Barel, C.J.A. 1973. Studies on dispersal of *Adoxophyes orana* F.V.R. in relation to the population sterilization technique. Mededelingen Landbouwsch. Wageningen 73:1–107.
- Batzer, H.O. 1968. Hibernation site and dispersal of spruce budworm larvae as related to damage of sapling balsam fir. Economic Entomology 61: 216–220.
- Bell, J.R., D.A. Bohan., E.M. Shaw & G.S. Weyman. 2005. Ballooning dispersal using silk: world fauna, phylogenies, genetics and models. Bulletin of Entomological Research 95:69–114.
- Chapman, J.W., D.R. Reynolds, & A.D. Smith. 2003. Vertical-looking radar: A new tool for monitoring high-altitude insect migration. Bioscience 53:503–511.
- Follner, K. & A.J. Klarenberg. 1995. Aeronautic behaviour in the wasp-like spider *Argiope bruennichi* (Scopoli) (Araneae, Argiopidae). In: V. Ruzicka (ed.) Proceedings of the 15th European Colloquium of Arachnology. Ceske, Budejovice. pp. 66–72.
- Goodacre, S. 2004. Population structure and evolutionary relationships among linyphiid spiders: a molecular analysis. In: Scientific abstracts of the 16th International Congress of Arachnology, Gent, Belgium 2–7 August 2004. p. 56. [http://allserv.rug.ac.be/~jpmalf/Abstracts%20Lezingen%20\(all\).pdf](http://allserv.rug.ac.be/~jpmalf/Abstracts%20Lezingen%20(all).pdf)
- Greenstone M.H., C.E. Morgan, A.L. Hultsch, R.A. Farrow & J.E. Dowse. 1987. Ballooning spiders in Missouri, USA, and New South Wales, Australia: family and mass distributions. Journal of Arachnology 15:163–170.

- Humphrey, J.A.C. 1987. Fluid mechanical constraints on spider ballooning. *Oecologia* 73:469–477.
- Jung, C. & B.A. Croft. 2001. Aerial dispersal of phytoseiid mites (Acari: Phytoseiidae): estimating falling speed and dispersal distance of adult females. *Oikos* 94:82–190.
- MacCook, H.C. 1877. The aeronautic flight of spiders. *Proceedings of the Academy of Sciences of Philadelphia* 1877:308–312.
- McCullagh, P. & J.A. Nelder. 1989. *Generalized Linear Models*, 2nd edition ed., Chapman and Hall.
- McManus, M.L. & C.L. Mason. 1983. Determination of the settling velocity and its significance to larval dispersal of the gypsy moth (Lepidoptera: Lymantridae). *Environmental Entomology* 12 pp 270–272.
- Mitchell, R.G. 1979. Dispersal of early instars of the Douglas-fir tussock moth. *Annals of the Entomological Society of America* 72:291–297.
- Okuma, C. & R. Kisimoto. 1981. Air borne spiders collected over the East China Sea. *Japanese Journal of Applied Entomology and Zoology* 25: 296–298.
- Osborne, J.L., S.J. Clark, R.J. Morris, I.H. Williams, J.R. Riley, A.D. Smith, D.R. Reynolds & A.S. Edwards. 1999. A landscape-scale study of bumble bee foraging range and constancy, using harmonic radar. *Journal of Applied Ecology* 36: 519–533.
- Ramachandran, R. 1987. Terminal velocity of the first instar *Ectropis excursia* (Guenee) (Lepidoptera: Geometridae). *Proceedings of the Indian Academy of Sciences (Animal Science)* 96:673–678.
- Schneider, J.M., J. Roos, Y. Lubin & J.R. Henschel. 2001. Dispersal of *Stegodyphus dumicola* (Araneae, Eresidae): they do balloon after all! *Journal of Arachnology* 29:114–116.
- Suter, R.B. 1991. Ballooning in spiders: results of wind tunnel experiments. *Ethology, Ecology & Evolution* 3:13–25.
- Suter, R.B. 1992. Ballooning: data from spiders in freefall indicate the importance of posture. *Journal of Arachnology* 20:107–113.
- Suter, R.B. 1999. An aerial lottery: the physics of ballooning in a chaotic atmosphere. *Journal of Arachnology* 27:281–293.
- Thomas, C.F.G., P. Brain & P.C. Jepson. 2003. Aerial activity of linyphiid spiders: modelling dispersal distances from meteorology and behaviour. *Journal of Applied Ecology* 40:912–927.
- Yoshimoto, C.M. & J.C. Gressitt. 1960. Trapping of air borne insects on ships in the Pacific (part 3). *Pacific Insects* 2:239–243.

Manuscript received 16 November 2004, revised 10 July 2005.